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SPATIAL AND TEMPORAL VARIATION IN DIETS OF SPOTTED OWLS IN WASHINGTON

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Abstract.—We studied diets of Northern Spotted Owls (*Strix occidentalis caurina*) in three different regions of Washington State during 1983–96. Northern flying squirrels (*Glaucomys sabrinus*) were the most important prey in most areas, comprising 29–54% of prey numbers and 45–59% of prey biomass. Other important prey included snowshoe hares (*Lepus americanus*), bushy-tailed woodrats (*Neotoma cinerea*), boreal red-backed voles (*Clethrionomys gapperi*), and mice (*Peromyscus maniculatus, P. oreas*). Nonmammalian prey generally comprised less than 15% of prey numbers and biomass. Mean prey mass was 111.4 ± 1.5 g on the Olympic Peninsula, 74.8 ± 2.9 g in the Western Cascades, and 91.3 ± 1.7 g in the Eastern Cascades. Diets varied among territories, years, and seasons. Annual variation in diet was characterized by small changes in relative occurrence of different prey types rather than a complete restructuring of the diet. Predation on snowshoe hares was primarily restricted to small juveniles captured during spring and summer. Mean prey mass did not differ between nesting and nonnesting owls in 19 of 21 territories examined. However, the direction of the difference was positive in 15 of the 21 cases (larger mean for nesting owls), suggesting a trend toward larger prey in samples collected from nesting owls. We suggest that differences in diet among years, seasons, and territories are probably due primarily to differences in prey abundance. However, there are other factors that could cause such differences, including individual variation in prey selection, variation in the timing of pellet collections, and variation in prey accessibility in different cover types.

Key Words: *Northern Spotted Owl*; Strix occidentalis caurina; *diet*; *predation*; *prey selection*; *Washington.*

Variación espacial y temporal en las dietas de *Strix occidentalis caurina* en Washington

Resumen.—Estudiamos las dietas de *Strix occidentalis caurina* en tres regiones diferentes del Estado de Washington durante 1983–96. *Glaucomys sabrinus* fue la presa mas importante en la mayoría de las áreas, representando 29–54% del número de presas y el 45–59% de la biomasa. Las presas importantes incluyeron *Lepus americanus, Neotoma cinerea, Clethrionomys gapperi, Peromyscus maniculatus, P. oreas.* Otras presas generalmente incluyeron menos del 15% del total de la biomasa. El promedio de la masa de presas fue de 111.4 ± 1.5 g en la Península Olímpica, 74.8 ± 2.9 g en las Cascadas Oeste y 91.3 ± 1.7 g en el este de la Península Olímpica. Las dietas variaron entre territorios, años y estaciones. La variación anual en la dieta fue caracterizada por los pequeños cambios en la ocurrencia relativa de diferentes tipos de presa en lugar de una reestructuración de la dieta. La depredación de *Lepus americanus* estuvo restringida a pequeños juveniles capturados durante la primavera y el verano. La media de la masa no

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difirió entre los buhos en anidación y los que no anidaron en 19 de los 21 casos (la media fue mayor para buhos en anidación), lo cual sugiere una tendencia hacia presas mayores en las muestras colectadas de los buhos en anidación. Sugerimos que las diferencias de las dietas entre años, estaciones y territorios se deben principalmente a las diferencias en la abundancia de las presas. Sin embargo existen otros factores que pueden causar estas diferencias, incluyendo la variación individual en la selección de presas, en el momento de la recoleccion de egagrópilas y la variación en la accesibilidad de presas en distintos tipos de cobertura.

[Traducción de César Márquez]

The Spotted Owl (*Strix occidentalis*) is primarily a predator of nocturnal mammals, but also feeds on a variety of birds, reptiles, amphibians, and insects (Forsman et al. 1984, Verner et al. 1992, Gutiérrez et al. 1995). Its diet varies considerably among regions, depending on prey availability (Laymon 1988, Ganey 1992, Verner et al. 1992, Ward and Block 1995, Duncan and Sidner 1990). In the coniferous forests of the Pacific Northwest, northern flying squirrels (*Glaucomys sabrinus*) and/or woodrats (*Neotoma* spp.) comprise the bulk of the diet in most areas (Barrows 1980, Forsman et al. 1984, Ward 1990, Ward and Block 1995, Bevis et al. 1997). Although regional differences in diets of Spotted Owls have been documented in many areas, variation in diet among territories, years, or seasons has received considerably less attention (Forsman 1980, Forsman et al. 1984, Laymon 1988, Thrailkill and Bias 1989, Ward 1990, Ganey 1992).

During studies of habitat use and demography of Northern Spotted Owls (*S. o. caurina*) in 1983–96, we collected regurgitated pellets from owl territories in three different geographic areas in Washington. Brief summaries of some of these data were presented in Forest Service management plans (Thomas et al. 1990) or in presentations at scientific meetings (Forsman et al. 1991), but the data have never been fully analyzed or presented. In this paper, we use the data from all three regions to assess differences in diet among regions and among owl territories within regions. We also examine annual and seasonal variation in diet and compare diets of nesting and nonnesting owls.

STUDY AREAS AND METHODS

The three study areas were the Olympic Peninsula, western Cascades, and eastern Cascades (Fig. 1). The Olympic Peninsula study area included the Olympic National Forest and National Park, plus adjacent lands administered by the Washington Department of Natural Resources. The western Cascades study area included samples of owls on the west slope of the Cascades Range, primarily on the Gifford Pinchot and Mt. Baker-Snoqualmie National Forests. The eastern Cascades study area was located on the Wenatchee National Forest on the east slope of the Cascades Range in central Washington. All study areas were characterized by steep, mountainous terrain, and were covered predominantly by conifer forests. The Olympic Peninsula and western Cascades study areas were characterized by forests of western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), and Pacific silver fir (*Abies amabilis*). The eastern Cascades study area was characterized by mixed-conifer forests of grand fir (*Abies grandis*), Douglas-fir, ponderosa pine (*Pinus ponderosa*), and western larch (*Larix occidentalis*) (Franklin and Dyrness 1973, Henderson et al. 1986). Forests on all areas consisted of a mosaic of different age classes and structural types that resulted from fire, windstorms, disease, and logging (Franklin and Dyrness 1973, Henderson et al. 1986).

Because of considerable differences in climate and vegetation, we subdivided the Olympic study area into eastern and western subprovinces for some comparisons of diet (Fig. 1). The western subprovince was characterized by high annual precipitation (360–480 cm/yr) with forests dominated by western hemlock and western redcedar. The eastern subprovince was characterized by comparatively less precipitation (40–200 cm/yr) with forests dominated by Douglas-fir (Henderson et al. 1986).

Collection of pellets was incidental to our main objectives, but we made a concerted effort to sample a large number of owl territories, and to clean roosts on a regular basis. All analyses were based on estimates of numbers or biomass of prey in pellets. We did not estimate the number of pellets collected or percent frequency of prey occurrence in individual pellets, because pellets were frequently fragmented and intermixed with other pellets under roosts. Numbers of prey were estimated by counting skulls, mandibles, bones of the appendicular skeleton, or pieces of exoskeleton, whichever gave the highest count for a particular species. In a few cases, we identified prey based on hair or feather samples, but this was rarely necessary, as we were usually able to identify prey based on bones. To avoid double-counting large animals that might appear in several pellets, we combined remains from multiple pellets collected at the same roost during the same time period.

Biomass of prey was estimated by multiplying the number of individuals by the mean mass of each species Estimates of mean mass for individual species were based on a variety of sources, including Forsman et al. (1984), Dunning (1993), museum specimens, and specimens that we collected on our study areas. Because most of the snowshoe hares (*Lepus americanus*), mountain beaver (*Aplodontia rufa*), and Blue Grouse (*Dendragapus obscurus*) in pellets were small juveniles, we estimated mass of each

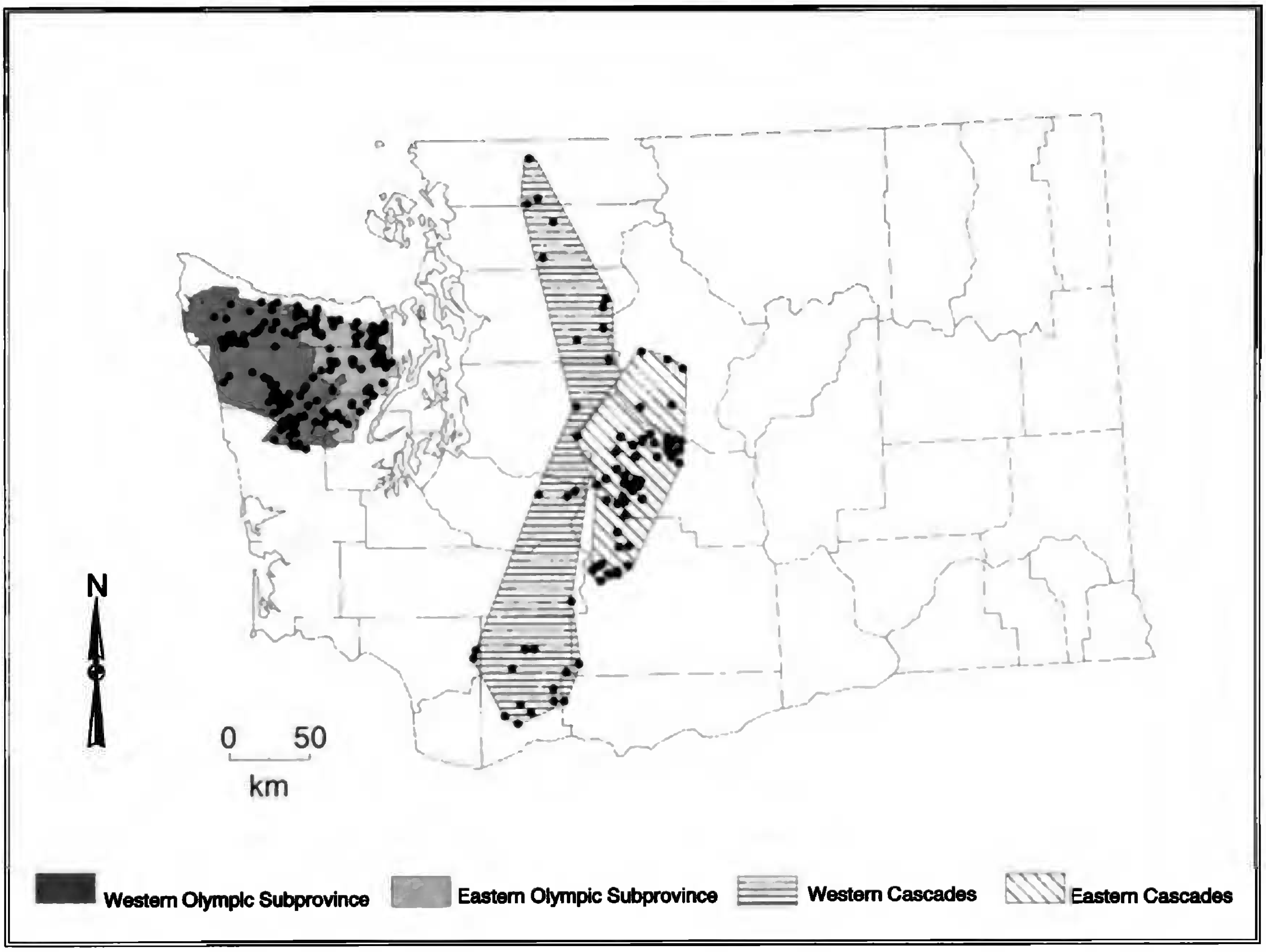

Figure 1. Three study areas in Washington where information was collected on the diet of Northern Spotted Owls, 1983–96. Symbols indicate locations of owl territories where pellets were collected. The Olympic Peninsula was subdivided into two subprovinces for some analyses, as indicated by the line separating the eastern and western subprovinces.

individual of these species by comparing size of bones in pellets with bones from specimens of known mass in a reference collection. In these cases, we made the simplifying assumption that mass was linearly correlated with the size of the bones in the pellets.

Most pellets were collected during the breeding season (March–August), when roosts used by adults and their offspring were concentrated in a small area around the nest tree or traditional nest area. During that period, we visited roosts at intervals of 2–6 wk to relocate owls and collect pellets. Data on diet during fall and winter (September–February) were obtained primarily from pellets of radio-marked owls in the western Olympic subprovince and eastern Cascades.

We estimated diets separately for each owl territory with $N \geq 20$ prey. Territories with <20 prey items were lumped into one sample and treated as a single "composite territory." Then, we averaged across territories to estimate the mean percent occurrence of each prey species in the diet in each study area (Swanson et al. 1974). Inclusion of the "composite territory" data as a single sample allowed us to use all of the data in the analysis, while avoiding the possibility that territories with small samples would carry the same weight as territories with large samples.

We used one-way analysis of variance tests (ANOVA) to determine which prey types differed among groups. We used *t*-tests or ANOVA to test the null hypothesis that mean prey size did not differ among years or between nesting and nonnesting owls. Chi-square tests were used to examine annual variation in composition of the diet and to test for differences in proportions of nocturnal and diurnal prey in diets of nesting and nonnesting owls.

Because of small sample size, χ^2 tests of variation among territories were based on all data from each territory, regardless of the years of data collection. All comparisons of annual, seasonal, and territorial differences in diet were limited to the Olympic Peninsula and eastern Cascades study areas, where samples were largest. Program SPSS (Norusis 1990) was used for all statistical analyses. All means are expressed as $\bar{x} \pm$ SE.

Table 1. Mean percent of prey numbers in diets of Northern Spotted Owls in three different regions of Washington, 1983–96. Standard errors indicate variation among owl territories. Number of owl territories sampled and total number of prey are in parentheses.

SPECIES	OLYMPIC PENINSULA (151:4238)[a] $\bar{x} \pm$ SEM	WESTERN CASCADES (57:638) $\bar{x} \pm$ SEM	EASTERN CASCADES (34:1867) $\bar{x} \pm$ SEM
Mammals	93.2 ± 0.54	91.5 ± 2.23	85.0 ± 3.14
Sorex spp.[b]	0.8 ± 0.18	3.8 ± 1.59	1.4 ± 0.36
Scapanus spp.[b]	0.3 ± 0.11	0.7 ± 0.67	0.3 ± 0.22
Ochotona princeps[c]		3.0 ± 0.98	0.3 ± 0.16
Lepus americanus	6.3 ± 0.74	1.9 ± 0.61	3.6 ± 0.64
Tamias spp.[d]	0.5 ± 0.13	1.9 ± 1.03	1.5 ± 0.38
Tamiasciurus douglasii	2.3 ± 0.31	0.6 ± 0.25	1.2 ± 0.35
Glaucomys sabrinus	54.3 ± 1.70	29.3 ± 4.12	40.7 ± 2.38
Thomomys spp.[e]	tr[f]	6.9 ± 3.24	4.3 ± 0.99
Peromyscus spp.[g]	11.3 ± 1.03	15.2 ± 3.62	6.5 ± 0.70
Neotoma cinerea	5.3 ± 0.94	1.3 ± 0.68	8.7 ± 1.40
Clethrionomys gapperi	5.8 ± 0.74	10.3 ± 3.02	6.4 ± 1.28
Phenacomys intermedius	0.2 ± 0.09	3.7 ± 3.38	0.8 ± 0.34
Microtus spp.[b]	1.7 ± 0.27	5.7 ± 2.59	1.9 ± 0.45
Other mammals[b]	4.4 ± 0.57	7.2 ± 1.12	7.4 ± 0.99
Birds[b]	6.4 ± 0.52	6.0 ± 1.53	4.4 ± 0.55
Amphibians[b]	0.1 ± 0.05		
Insects[b]	0.4 ± 0.11	2.5 ± 1.22	10.6 ± 3.34
Total	100.0	100.0	100.0

[a] (After lumping data from territories with <20 prey, the number of territories used to estimate means was 64 on the Olympic Peninsula, 12 in the western Cascades, and 26 in the eastern Cascades).

[b] Species not specifically identified in table and that generally provided less than 1% of total biomass in the diet were: mammals (*Sorex trowbridgii, S. monticolus, S. vagrans, Neurotrichus gibbsii, Scapanus orarius, S. townsendii, Myotis spp., Lasionycteris noctivagans, Eptesicus fuscus, Aplodontia rufa, Thomomys mazama, T. talpoides, Microtus longicaudus, M. oregoni, M. richardsoni, M. townsendii, Zapus trinotatus, Mustela erminea*); birds (*Dendragapus obscurus, Columba fasciata, Otus kennicottii, Glaucidium gnoma, Aegolius acadicus, Dryocopus pileatus, Sphyrapicus ruber, Picoides villosus, Colaptes auratus, Cyanocitta stelleri, Perisoreus canadensis, Catharus spp., Ixoreus naevius, Turdus migratorius, Sitta canadensis, Troglodytes troglodytes, Regulus satrapa, Parus rufescens, Loxia curvirostra, Coccothraustes vespertinus, Junco hyemalis, Nuttalornis borealis*); amphibians (*Rana* spp.); insects (*Cyphoderris monstrosa, Formica fusca, Ergates spiculatus*).

[c] Did not occur on the Olympic Peninsula.

[d] All *Tamias townsendii* except in the eastern Cascades study area where diet included both *T. townsendii* and *T. amoenus*.

[e] *T. mazama* in Olympic Peninsula, *T. talpoides* in Cascades.

[f] tr = trace (<0.05% of total prey numbers).

[g] All *P. maniculatus* except in Olympic Peninsula where both *P. maniculatus* and *P. keeni* were present and could not be separated based on skeletal remains.

RESULTS

Regional Variation. We obtained pellets from 151 owl territories on the Olympic Peninsula, 57 territories in the eastern Cascades, and 34 territories in the western Cascades. Each territory was occupied by a uniquely banded pair of owls that was regularly found in the same area, usually in more than one year. The mean number of prey items collected per territory was 27.1 ± 2.39 (range = 1–249). We identified ≥20 prey items at 98 territories. We identified a total of 6743 prey and at least 57 species (31 mammals, 22 birds, 1 amphibian, and 3 insects) (Tables 1 and 2).

Samples from the three study areas were similar in that they were primarily comprised of forest mammals, with the northern flying squirrel predominating in all areas, both in terms of numbers and biomass (Tables 1 and 2). Other mammals that were common in most samples were boreal red-backed voles (*Clethrionomys gapperi*), mice (*Peromyscus* spp.), and snowshoe hares. Bushy-tailed woodrats (*Neotoma cinerea*) and gophers (*Thomomys* spp.) were rare in the diet in some regions, but comprised over 5% of prey numbers in others (Tables 1 and 3). Some pairs in the Cascades captured considerable numbers of pikas (*Ochotona princeps*),

Table 2. Mean percent of prey biomass in diets of Northern Spotted Owls in three different regions of Washington, 1983–96. Standard errors indicate variation among owl territories. Number of owl territories sampled and total prey biomass (g) in parentheses.

SPECIES	OLYMPIC PENINSULA (151:471 757)[a] $\bar{x}$ ± SEM	WESTERN CASCADES (57:47 738) $\bar{x}$ ± SEM	EASTERN CASCADES (34:70 539) $\bar{x}$ ± SEM
Mammals	95.2 ± 0.48	94.5 ± 1.62	95.8 ± 0.63
Sorex spp.	tr[b]	0.5 ± 0.16	0.1 ± 0.02
Scapanus spp.	0.2 ± 0.06	0.5 ± 0.53	0.2 ± 0.18
Ochotona princeps[c]		6.0 ± 2.05	0.5 ± 0.30
Lepus americanus	16.3 ± 1.72	8.9 ± 2.86	9.4 ± 1.82
Tamias spp.	0.3 ± 0.09	1.9 ± 1.03	1.0 ± 0.25
Tamiasciurus douglasii	4.1 ± 0.56	1.5 ± 0.60	2.2 ± 0.65
Glaucomys sabrinus	58.6 ± 2.31	45.3 ± 4.91	52.5 ± 2.38
Thomomys spp.	tr	8.7 ± 4.09	3.7 ± 0.88
Peromyscus spp.	2.5 ± 0.28	4.9 ± 1.32	1.9 ± 0.29
Neotoma cinerea	9.8 ± 1.64	4.5 ± 2.42	18.1 ± 2.63
Clethrionomys gapperi	1.2 ± 0.17	3.6 ± 1.21	2.2 ± 0.56
Phenacomys intermedius	0.1 ± 0.03	2.0 ± 1.88	0.6 ± 0.36
Microtus spp.	0.4 ± 0.09	2.6 ± 1.54	0.5 ± 0.11
Other mammals	1.6 ± 0.22	3.6 ± 0.85	2.9 ± 0.50
Birds	4.8 ± 0.48	5.5 ± 1.62	3.5 ± 0.56
Amphibians	tr		
Insects	tr	tr	0.7 ± 0.49
Total	100.0	100.0	100.0

[a] After lumping data from territories with <20 prey, the number of territories used to estimate means was 64 in the Olympic Peninsula, 12 in the western Cascades, and 26 in the eastern Cascades.

[b] tr = trace (<0.05% of total biomass).

[c] Did not occur on Olympic Peninsula.

Table 3. Mean percent of prey numbers in diets of Northern Spotted Owls in the eastern and western subprovinces of the Olympic Peninsula, Washington, 1983–96. Standard errors reflect variation among owl territories.

SPECIES/GROUP	WESTERN SUBPROVINCE $\bar{x}$ ± SEM[a]	EASTERN SUBPROVINCE $\bar{x}$ ± SEM	$F_{1,62}$	P
Mammals	93.3 ± 0.81	93.2 ± 0.71	0.1	0.79
Glaucomys sabrinus	63.3 ± 1.90	45.2 ± 1.69	50.3	<0.001
Clethrionomys gapperi	1.2 ± 0.41	10.3 ± 0.86	92.3	<0.001
Lepus americanus	4.1 ± 0.67	8.5 ± 1.23	9.7	0.003
Tamiasciurus douglasii	2.1 ± 0.53	2.4 ± 0.32	0.2	0.70
Microtus spp.	0.9 ± 0.35	2.5 ± 0.37	9.5	0.003
Neotoma cinerea	1.1 ± 0.54	9.6 ± 1.48	28.8	<0.001
Peromyscus spp.	15.6 ± 1.46	7.0 ± 0.99	23.9	<0.001
Other mammals	5.0 ± 0.71	7.6 ± 0.91	5.1	0.03
Birds	6.4 ± 0.78	6.3 ± 0.71	0.001	0.98
Frogs/Insects	0.3 ± 0.15	0.6 ± 0.20	1.5	0.223
Totals:	100.0	100.0		

[a] Number of territories sampled in the western and eastern subprovinces was 72 and 79, respectively, but after lumping data from territories with <20 prey, the number of territories used to estimate means was 32 in each subprovince.

but pikas did not occur on the Olympic Peninsula (Tables 1 and 2). A variety of shrews (*Sorex* spp.), moles (*Scapanus* spp.), diurnal squirrels (*Tamias* spp., *Tamiasciurus douglasii*), microtines, and an occasional weasel (*Mustela erminea*) or bat (Chiroptera) made up the balance of the mammalian prey in the diet (Tables 1 and 2).

Nonmammalian prey included a variety of birds, insects, and amphibians generally comprising <15% of prey numbers, and <5% of biomass (Tables 1 and 2). Insects were common in the diet in the comparatively xeric eastern Cascades study area, but were rare in the diet in the cool, damp forests of the Olympic Peninsula (Table 1).

Mean mass of individual prey was 111.4 ± 1.5 g on the Olympic Peninsula, 74.8 ± 2.9 g in the western Cascades, and 91.3 ± 1.7 g in the eastern Cascades. Mean mass of prey did not differ between nesting and nonnesting years at 19 of 21 territories examined (*t*-tests, all but two *P*-values > 0.05). However, in 15 of the 21 territories, the direction of the difference was positive (larger means for nesting pairs).

Nocturnal animals comprised 93.7% of prey numbers in the Olympic Peninsula, 88.3% in the western Cascades, and 92.1% in the eastern Cascades. There was no difference in the relative proportions of nocturnal and diurnal prey in diets of nesting and nonnesting owls in either the Olympic Peninsula (χ^2_1 = 0.126, P = 0.72) or eastern Cascades (χ^2_1 = 3.42, P = 0.06).

On the Olympic Peninsula, mammals dominated the diet in both subprovinces, but the composition of the diet differed between subprovinces (Table 3). The most noticeable difference was that bushy-tailed woodrats and red-backed voles were relatively rare in the diet in the western subprovince compared to the eastern subprovince (Table 3). In the eastern subprovince, woodrats were particularly common in the diets of owls that occupied areas characterized by steep canyons with extensive areas of rock outcrops, cliffs, and talus. In the latter areas, diets of some pairs included 20–40% woodrats by numbers. Other differences between the two subprovinces were that flying squirrels and mice (*Peromyscus* spp.) were more common in the diet in the western subprovince, whereas snowshoe hares were more common in the diet in the eastern subprovince (Table 3).

Variation Among Territories. Composition of the diet differed among territories in the eastern Cascades (χ^2_{50} = 2371.1, P < 0.001) and in both subprovinces of the Olympic Peninsula (eastern subprovince χ^2_{62} = 110.4, P < 0.001; western subprovince χ^2_{62} = 116.6, P < 0.001). Although many of the differences among territories were fairly small, there were some extreme differences as well. Examples included the occasional pairs on the Olympic Peninsula that had diets dominated by woodrats or snowshoe hares.

Annual Variation. Composition of the diet differed among years in five of 17 territories where we had annual samples ≥20 in two or more years (χ^2 *P*-values < 0.05). In all cases, annual variation appeared to reflect small among-year fluctuations in the relative percentages of different prey types rather than dramatic shifts from one prey type to another. For example, the northern flying squirrel was the primary source of biomass in all years at 13 of the 17 territories examined, and bushy-tailed woodrats were the major source of biomass in all years at one territory. At three of the 17 territories, flying squirrels were the primary source of biomass in most years, but snowshoe hares were the primary source of biomass in some years. Mean mass of individual prey varied among years on the eastern Cascades study area ($\bar{x}$ = 99.4 ± 4.5 g, $F_{5,1,772}$ = 6.40, P < 0.001), but did not differ among years on the Olympic Peninsula ($\bar{x}$ = 110.5 ± 2.4 g, $F_{9,4,095}$ = 1.56, P = 0.12).

Seasonal Variation. The proportion of flying squirrels in the diet increased slightly during winter, whereas predation on insects, gophers, and snowshoe hares was largely restricted to the spring, summer, and early fall (Table 4). Of 305 snowshoe hares in the combined sample from all study areas, 289 (95%) were juveniles or subadults with mass ≤600 grams, and 99.3% were captured between 1 March–30 September. Species that hibernated or spent the winter under the snow (e.g., chipmunks, pikas) were absent from the diet from approximately October–March.

DISCUSSION

Our results were largely consistent with previous studies of the Northern Spotted Owl in that the diet included a broad range of prey, but was predominantly composed of flying squirrels and/or woodrats (Barrows 1980, Forsman et al. 1984, Richards 1989, Ward 1990, Ward et al. 1998, Bevis et al. 1997). One hypothesis that has been frequently repeated in the literature is that Spotted Owls forage selectively on medium-sized mammals (flying squirrels, woodrats, lagomorphs), but also take a broad

Table 4. Composition of the diet (% of numbers) of Northern Spotted Owls during the breeding season (March–August) and winter (September–February) in the eastern Cascades study area and western subprovince of the Olympic Peninsula study area Washington. Samples sizes are in parentheses.

	EASTERN CASCADES		WESTERN OLYMPIC PENINSULA	
SPECIES/GROUP	BREEDING SEASON (1764)	WINTER (103)	BREEDING SEASON (1407)	WINTER (173)
Mammals	85	96	94	97
Glaucomys sabrinus	43	52	61	74
Thomomys spp.	4	2	0	0
Peromyscus spp.	6	6	15	9
Neotoma cinerea	7	15	2	1
Lepus americanus	4	1	6	1
Other mammals	21	20	10	12
Birds	4	4	6	3
Other (insects, frogs)	11	0	tr[a]	0
Totals	100	100	100	100

[a] tr = trace (<0.05% of total prey numbers).

range of prey as they are encountered (Forsman et al. 1984, Verner et al. 1992, Ward et al. 1998, Carey et al. 1995, Gutiérrez et al. 1995). Although our data seem to fit this hypothesis, we had no information on the relative accessibility or ease of capture of the many different kinds of prey captured by the owls. Thus, we could not prove that the owls actually selected their prey in a manner disproportionate to what was available or accessible to them.

The preponderance of nocturnal prey in the diet indicated that the majority of foraging occurred at night, an observation that agrees with previous studies of Spotted Owls (e.g., Forsman et al. 1984, Laymon 1988, 1991, Sovern et al. 1994). Although approximately 8.5% of the prey captured by owls on our study areas were diurnal birds or mammals, we suspect that some of these were captured at night or during periods of crepuscular activity. However, there is no question that some prey were captured during the day, as we observed numerous cases in which Spotted Owls captured, or tried to capture, prey during the day (e.g., see Sovern et al. 1994).

The high proportion of arboreal or semiarboreal mammals in diets of Spotted Owls in the Pacific Northwest suggests that the owls spend much of their time foraging in the forest canopy (Forsman et al. 1984). This behavior is well-suited for existence in dense forests, where considerable prey biomass is found in the forest canopy (Carey 1991, Carey et al. 1992, Rosenberg and Anthony 1992), and where the forest floor is often obscured by dense shrubs. At least some other large forest owls appear to have adopted similar foraging strategies. For example, Powerful Owls (*Ninox strenua*) feed primarily on arboreal marsupials (Seebeck 1976, James 1980, Kavanagh 1988), and diets of Rufous-legged Owls (*Strix rufipes*) include high proportions of arboreal or scansorial mammals in some areas (Martinez and Jaksic 1996, Díaz 1999).

Regional variation in utilization of different prey types in Washington was in some cases due to regional differences in prey distribution. For example, pikas were locally common in talus slopes in the Cascades Mountains, but did not occur on the Olympic Peninsula (Dalquest 1948). Gophers, which were numerically common in samples from the eastern and western Cascades study areas, were rare in the diet on the Olympic Peninsula, apparently because gophers were uncommon or absent in the latter area (Dalquest 1948, Ingles 1965). Similarly, woodrats are apparently uncommon on the Olympic Peninsula except in steep, rocky canyons on the east side of the peninsula (Carey et al. 1999). The rarity of insects in the diet on the Olympic Peninsula also suggests that large crickets and beetles (e.g., *Cyphoderris monstrosa, Ergates spiculatus*) were much less abundant in that region than in the eastern Cascades.

In the southwestern U.S. and Sierra Nevada Mountains of California, bats are fairly common in diets of some pairs of Spotted Owls (Laymon 1988, Duncan and Sidner 1990, Ward and Block 1995). In comparison, bats were uncommon in our samples from Washington and in samples from Oregon (Forsman et al. 1984). We suspect these differences are due to variation in the relative abundance and accessibility of bats in the different regions. For example, in Oregon and Washington, bats are not available as prey during winter because they either hibernate or migrate. In contrast, some species of bats in southwest Arizona are active throughout the year, and are locally abundant in cliffs and caves where the owls roost and nest (Duncan and Sidner 1990).

A consistent finding in our study was that diets varied among territories, even within the same forest type and geographic area. Similar observations have been reported for Spotted Owls in other regions (Laymon 1988, Ward 1990, Ganey 1992, Ward et al. 1998). Annual and territorial variation in diet of predatory birds is well-documented, and is often attributed to spatial or temporal variation in prey abundance (Rusch et al. 1972, Marti 1988, Pietiainen 1989, Hakkarainen and Korpimäki 1994, Marti and Kochert 1996, Gende and Wilson 1997, Steenhof et al. 1997). In our study, we believe that much of the variation among pairs was due to spatial variation in prey abundance (e.g., woodrats on the Olympic Peninsula). However, numerous other factors could have caused variation in diets, including variation among individual owls, seasonal or annual variation in the timing of pellet collections, and differences in prey accessibility in different vegetation types. These potential sources of variation are impossible to control in field studies like ours and may confound attempts to determine relationships between prey abundance and prey selection.

Although we observed some annual variation in diet of individual pairs, none of the differences were so large as to suggest dramatic variation in the relative abundance of different prey among years. However, there were a few territories where flying squirrels and snowshoe hares alternated as the predominant source of biomass in different years, suggesting that prey abundance may have varied among years in at least some territories. Our samples from individual territories were too small to determine if these results could have been influenced by turnover of resident owls or slight differences in timing of pellet collections.

Seasonal changes in diet in our study were similar to patterns observed in previous studies, in that predation on flying squirrels increased during fall and winter, while predation on snowshoe hares was limited primarily to small juveniles captured during spring and summer (Forsman et al. 1984, Forsman et al. 1994). Seasonal predation on juvenile lagomorphs has been described in many other owls, including Tawny Owls (*Strix aluco*; Southern 1970), Northern Hawk Owls (*Surnia ulula*; Rohner et al. 1995), Great Grey Owls (*Strix nebulosa*; Mikkola 1983), Barn Owls (*Tyto alba*; Marti 1988), Long-eared Owls (*Asio otus*; Marti 1976), and Snowy Owls (*Nyctea scandiaca*; Watson 1970). This seasonal pattern reflects seasonal changes in abundance, but is probably also a function of the relative ease of capture of small, naive juveniles.

Our analysis, and similar analyses by Ward (1990), Ward et al. (1998), and Seamans and Gutiérrez (1999) did not indicate consistent differences in diet between nesting and nonnesting Spotted Owls. However, even though the differences were not significant in most cases, we did note that mean mass of prey in diets of nesting pairs was larger in 15 of 21 territories examined. This could be interpreted as a trend toward larger prey in diets of nesting owls, as was suggested by Barrows (1985, 1987) and Thrailkill and Bias (1989). We are not convinced that this is an appropriate interpretation because collections of pellets from nest areas may overestimate the number of large prey captured by nesting males. Male owls that are nesting probably eat many small prey while foraging, but deliver most large prey items (e.g., squirrels, woodrats, rabbits) to the nest or fledged young (Bull and Henjum 1990). Because of this bias, a mixture of male, female and juvenile pellets collected from nest areas should contain more large prey than would be found in the pellets of the male alone. The magnitude of this bias probably varies depending on the ratio of male pellets to pellets from females and young in a particular sample. Thus, contrary to Seamans and Gutiérrez (1999), we believe that analysis of prey remains in pellets may be a misleading method for comparing diets of nesting and nonnesting owls. This same bias could confound comparisons among years or among owl territories if some pairs are nesting and others are not.

Although some studies of radio-marked Spotted Owls have suggested fairly high levels of diurnal foraging by nesting individuals (Laymon 1988, 1991, Sovern et al. 1994), we found no differences in the proportion of nocturnal and diurnal prey in diets of nesting and nonnesting owls. We have no explanation for this apparent inconsistency, except to suggest that capture rates during the day may be so low that slight differences in diurnal foraging activity may not result in measurable differences in diet between nesting and nonnesting owls.

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